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SYMPATRIC CHARACTER CONVERGENCE BETWEEN TWO SPECIES OF CLOSELY RELATED GENERA OF PHOLADINAE (BIVALVIA: PHOLADIDAE) FROM THE EASTERN COAST OF INDIA

Tanmoy Hari[1]*, Subhendu Bardhan[1] & Debahuti Mukherjee[2]

ABSTRACT

Biological interaction between two ecologically related species in sympatry results mostly as character divergence, which is also known as ecological character displacement. However, there are reports of character convergence in areas of overlap. Here we present a case study of sympatric convergence and allopatric divergence in form between two species, *Barnea candida* (Linnaeus, 1758), and *Pholas orientalis* Gmelin, 1791.They are members of closely related genera of marine bivalves from the eastern coast of India. So far as we know, this is the first report of a biological interaction between marine living bivalves. These two species are mud-boring deposit feeders. All of the characters here analyzed to show character shifting have adaptive significance or are proxy data for trophic apparatus. The present study involves more than 1,200 specimens collected from three sympatric and three allopatric sites that range over 1,000 km. Statistical analyses reveal that *B.candida* diverges more from its allopatric position than *P. orientalis* in sympatry. Character displacement generally takes place in sympatry to avoid or minimize competition for similar resources. The present two species have similar reproductive and feeding strategies. They also have similar ecological requirements for food and habitat. Because of these ecological and functional constraints, *Barnea candida* and *Pholas orientalis* could not reduce competition by resource partitioning. Instead, they compete and hence converge.

Key words: boring bivalves, Indian coast, sympatric convergence, ecological constraints.

INTRODUCTION

Species living in any area are always subjected to natural selection pressure, which has both physicochemical and biological attributes. Even when physicochemical parameters remain more or less constant, two related species mutually react in sympatry. This is known as biological interaction between two related species (Schindel & Gould, 1977). In a majority of cases, as studied in terrestrial animals or plants, the common reaction is what is known as ecological character displacement (Brown & Wilson, 1956). These authors stated, "When two species of animals overlap geographically, their differences are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone" (p. 63). However, subsequent workers expanded this evolutionary process to include both divergence and convergence of relevant characters (Grant, 1972; Taper & Case, 1992). Divergent character displacement results from the fact that it allows competing species to reduce competition for resources, such as food and habitable space in sympatric areas. This is done by partitioning of the resources, which consequently leads to variation of characters related to foraging by the sympatric populations (Dunham et al., 1979; Schulter & McPhail, 1992; Robinson & Wilson, 1994; Scott & Foster, 2000).

This pattern of sympatric divergence and allopatric convergence has been observed in different organisms, including birds (Orians & Wilson, 1964; Grant, 1965, 1966), lizards (Schoener, 1970; Huey & Pianka, 1974), frogs (Blair, 1974), fishes (Schluter, 1994), tiger beetles (Pearson & Mury, 1979), plants (Grant (1994), and others (Dayan & Simberloff, 2005; and references therein).

However, biological interaction in sympatry can give rise to character convergence instead of displacement between two ecologically simi-

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[1]Department of Geological Sciences, Jadavpur University, Kolkata 700032, India
[2]Geological Survey of India, 15 Kyd Street, Kolkata 700016, India
*Corresponding author: tanmoy.hari@gmail.com

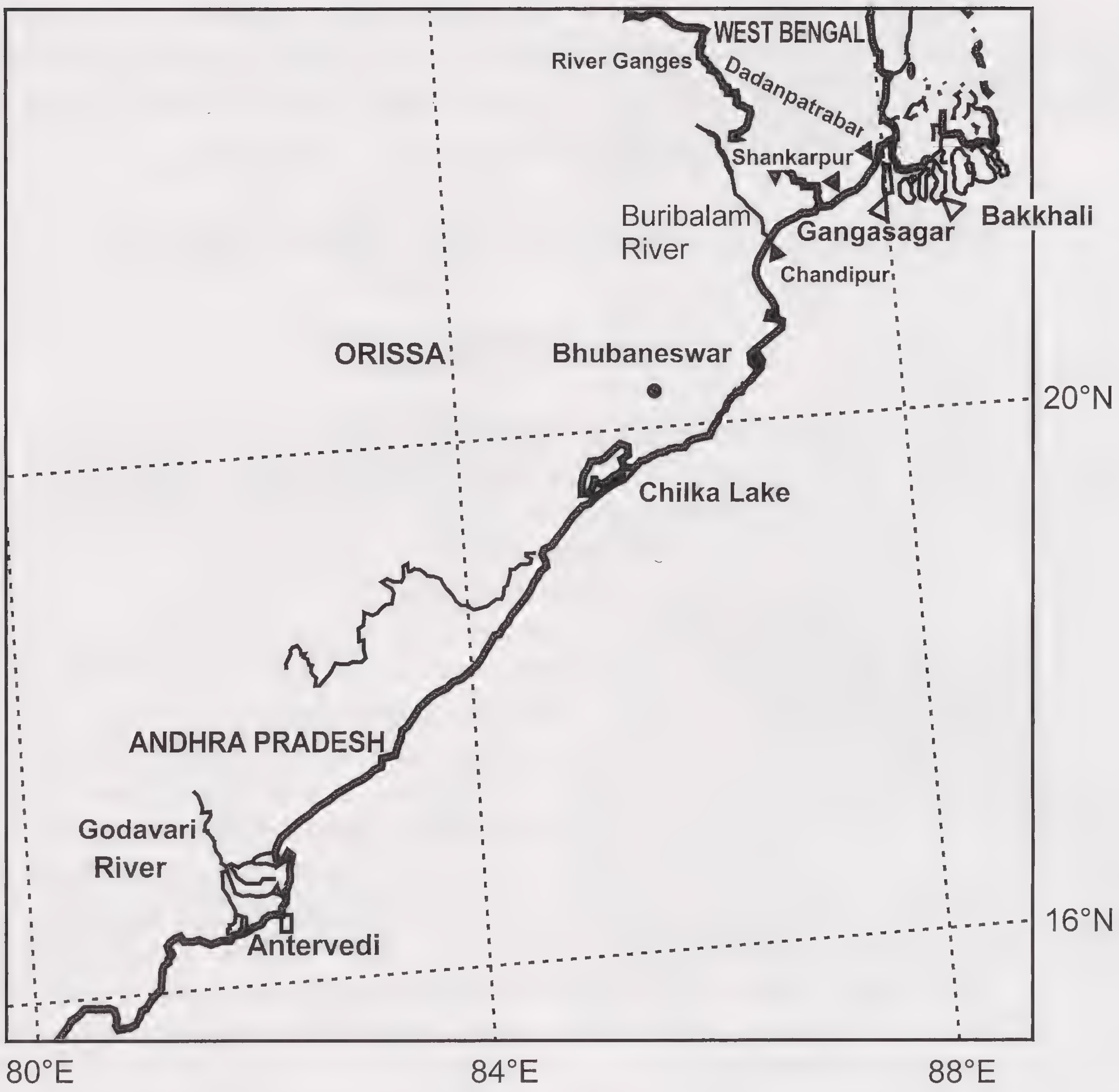

FIG. 1. Map of the coastline along eastern India, showing field sites of both sympatric (close triangle) and allopatric populations of *Barnea candida* (open triangle) and *Pholas orientalis* (rectangle).

lar species (Schoener, 1970; Grant, 1972, 1975; Wilson, 1975; Taper & Case, 1992). According to Cody (1973), character convergence can occur between closely related species or genera that can act in a very similar way if resources do not limit further population growth, and ecology or diet are very similar. He further stated that convergence is shown by characters of ecological significance. Convergence can also occur if sympatric populations try to monopolize habitats and convergent characters are related to territory establishment and maintenance (Cody, 1969, 1973; Grant, 1972; Arthur, 1982).

There are many theoretical models that explain both character displacement and convergence (Slatkin, 1980; Abrams, 1986, 1987; Taper & Case, 1992). But a general observation of these models is that under many circumstances at least the sizes of two competing taxa show parallelism or convergence rather than divergence (Dayan & Simberloff, 2005).

Molluscan examples of such biological interactions are now emerging. In a terrestrial gastropod community, two related species exhibit traditional allopatric convergence and sympatric divergence (Schindel & Gould, 1977). Subsequently, many workers studied land snails to demonstrate character displacement (Dayan & Simberloff, 2005), and some studies indicate that character displacement can be caused by environmental factors (Emberton, 1995). Marine examples of molluscan character displacement are available mainly from fossil taxa. Elredge (1968) studied character displacement in Pennsylvanian archeogastropod species. Sympatric character convergence has been studied by one of us (S. B.) along with others in Jurassic trigoniid bivalves (Rudra & Bardhan, 2006; Rudra et al., 2007), and eucycloceratiin ammonites (Jana et al., 2005). In the present endeavor, we have studied the interaction between two species of closely related genera of modern marine bivalves. This is the first known example of biological interaction between two established species of marine living Mollusca resulting in character convergence.

Barnea candida (Linnaeus, 1758) and *Pholas orientalis* Gmelin, 1791, are two boring Recent bivalves, belonging to the subfamily Pholadinae of the family Pholadidae (Turner, 1969). They are found in many areas of the world, but they have different distributional patterns on the eastern coast of India (Fig. 1). *Pholas orientalis* is restricted mainly to the southern part, whereas *B. candida* is found in the northeastern areas. The sympatric sites, where these two species live together, lie between. They are morphologically distinct and are well recognized in the literature (Turner, 1969). Here, we show that their morphological distinction becomes weak in sympatric populations, especially in size and other quantifiable morphological characters that have functional and ecological significance. Detailed statistical analyses involving univariate, bivariate, and multivariate methods support this observation.

Barnea candida and *Pholas orientalis* have similar ecological requirements for food and habitat. These constraints compel them to compete for the same resources, which perhaps results in the observed sympatric convergence.

MATERIALS AND METHODS

Several field trips were carried out in different seasons during 2005–2006. The studied area includes both allopatric and sympatric sites of *Barnea candida* and *Pholas orientalis*, ranging more than 1,000 km from their northeastern to southwestern limits. Allopatric sites of *Barnea candida* are Bakkhali and Gangasagar, which are located in the northeastern part of the studied area, whereas the only allopatric site of *P. orientalis,* Antarvedi, falls at the southern limit (Fig .1). About 1,200 samples were analysed. They were all dead and collected systematically. All of the samples were disarticulated in nature. We did not have any bias in collection. Where samples are sparse (e.g., Bakkhali and Chandipur), we collected all the samples encountered, including juveniles, sub-adults and adults. Where samples were plentiful (e.g., Gangasagar, Dadanpatrabar, Shankarpur, and Antervedi), we used a sampling design where we made randomly chosen 2 m x 2 m grids and collected all samples. We also collected valves that lay outside the grids, if they were of larger individuals, because one of our aims was to determine the change in body size in sympatry.

Preservation of the samples was very good. All of the delicate structural elements, for example, small anterior spines, ridges, apophyses, and extremely thin shells of both of the species, were still present in most specimens. These two species live within bottom-level community and do not have external ligaments, and therefore valves readily become disarticulated during exhumation after death. The presence of delicate structures suggests that the shells did not suffer much posthumous transport.

We do not claim that dead single valves we collected represent similar number of individuals. Theoretically, number of individuals should be half of the total number of single valves. But, as shells suffered postmortem transportation, ratios between left and right valves are not uniform in the collections. Left valves are generally more for both *Barnea candida* (ranges between 53.9% and 63.9%) and *Pholas orientalis* (52.3% to as high as 95.5% in allopetric Antervedi). Thus, it may be said that although studied 1,200 samples are completely disarticulated, they represent more than 600 individuals. Number of samples is thus quite sizable to quantify body size structures of living populations of two species.

The total number of hours spent searching for samples at a particular locality varied depending on local abundance of large adults and tide time. Total hours spent in searching samples were 12, 18, 14, 12, 48 and 12 for Bakkhali, Gangasagar, Dadanpatrabar, Shankarpur, Chandipur, and Antervedi, respectively.

We measured only the dead specimens, and the specimens can be time-averaged. Delicate shell characters cannot sustain long exposure to waves and currents for long. Even so, time-averaged death assemblages of marine molluscs could be more faithful representatives of the regional populations than living individuals (Kidwell & Flessa, 1995; Kidwell, 2001; Roy et al., 2003).

Barnea candida and *Pholas orientalis* are found only in muddy substrata of varying density. Muddy substrata are highly localized and are found only near estuary mouths. Because of their peculiar life mode, these two species have many functional morphological characters in common. Boring bivalves in general and pholadines in particular have a streamlined shape, extremely thin shells that are strongly inequilateral, gaping at both anterior and posterior ends, deep pallial sinuses, and small anteroventral spines for scraping within the stiff medium. These characters have functional significance, and some of them represent trophic

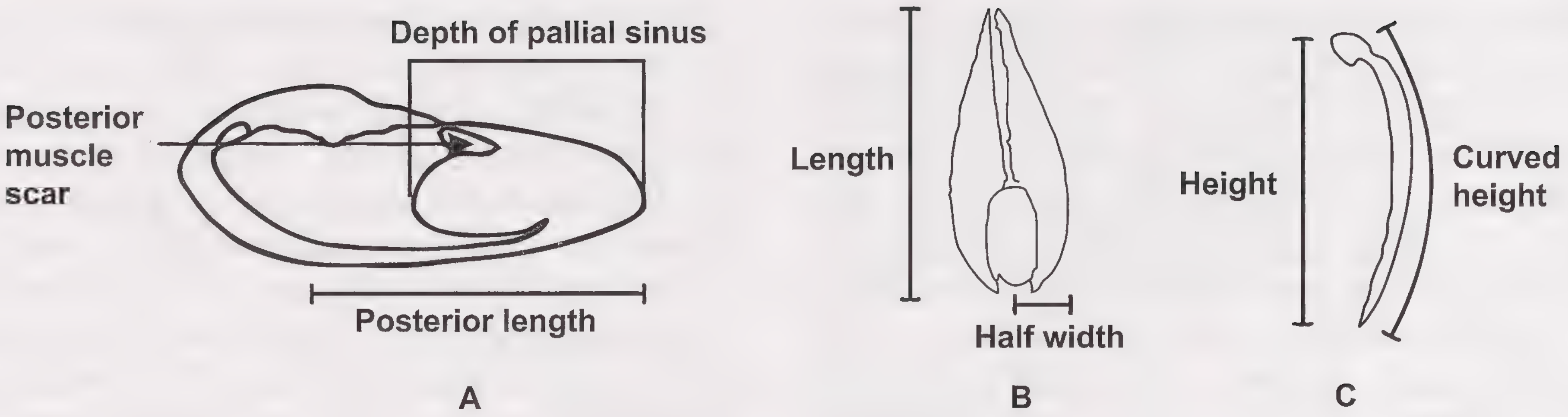

FIG. 2. General dimensions of pholadine bivalves measured in this study. A: lateral internal view; B: dorsal view; C: anterior transverse view.

structure. Pholadines are sessile benthic and deposit feeders (Stanley, 1970). They have long siphons used as trophic appendages to forage plant particulates from the sediment. The depth of the pallial sinus was used here as a proxy for the length of the siphons.

We have chosen seven characters to compare variation among allopatric and sympatric populations. These characters, we believe, have ecological and functional value, and *Barnea candida* and *Pholas orientalis* show interspecific diversity with respect to these characters. In addition, each also has its own genus-diagnostic, non-quantifiable stable characters, which make the two species taxonomically quite distinct. For example, *P. orientalis* has a pronounced smooth posterior end, a septate umbonal region, and spatulate apophyses, whereas *B. candida* has a simple umbo, rod-like apophyses, and entire ornamentation (Turner, 1969). These two species show convergence only in functional morphological characters, whereas the stable characters remain almost unchanged. The seven functional characters (Fig. 2) are:

1. Shell length – distance measured between the anterior and posterior tips.
2. Shell height – distance measured along the vertical line between umbo and ventral commissure.
3. Shell width – maximum width measured along the same plane where height has been measured. The value has been doubled to obtain the shell width of the intact animal.
4. Posterior length – distance measured between mid-umbonal line and posterior tip.
5. Depth of pallial sinus – distance measured between posterior end of the shell and point of maximum indentation of the pallial sinus.
6. Curved height – distance measured between umbo and ventral commissure along the shell surface.
7. Area of posterior muscle scar – product of the length along the maximum elongation of the muscle scar and the height perpendicular to it.

In addition, we have computed two shape indices, which are:

8. Relative inflation of the shell (shell width/shell height)
9. Relative convexity of the valve (shell height/curved height).

Because convergence in shape is not very much evident in multivariate analysis, as loadings of these shape data become masked by the influence of size data in first two discriminant functions, these characters are used only in univariate analyses.

From the univariate analyses, it is clear that the degree of convergence in all of the sympatric areas is not constant. To understand the nature of variation among sympatric areas, we also performed statistical analysis to determine the between-group Mahalanobis distances between each sympatric site with respect to allopatric sites.

Between-group variation between the two ecologically closely related species *Barnea candida* and *Pholas orientalis* has been studied in the allopatric and sympatric sites to understand and quantify the amount of morphological shifting. We have employed univariate (simple data display), bivariate (growth curves), and multivariate (Mahalanobis distance and discriminant function analysis) techniques to analyze the variation. Discriminant function analysis (DFA) involves group mean vectors, which are multivariate analogs of the means. Here DFA has been used to discriminate between *a priori* groups in terms of their group centroids to evaluate the patterns in morphological differences. The univariate data display the contribution of the individual variables to the multivariate distances.

TABLE 1. Mahalanobis distances among allopatric and sympatric populations of *Barnea candida and Pholas orientalis.* F values are shown in parentheses and are significant in 99% confidence level except in *P. orientalis* allopatric and sympatric populations.

	Barnea candida		*Pholas orientalis*	
	Sympatric	Allopatric	Sympatric	Allopatric
Barnea candida				
Sympatric	–	3.67210	9.78198	–
Allopatric	(8.74949)	–	–	19.81113
Pholas orientalis				
Sympatric	(29.33528)	–	–	1.25287
Allopatric	–	(25.49808)	(1.81384)	–

Most bivalves do not generally have any recognizable adult characters and growth is continuous. However, growth lines become crowded, and constrictions appear near the ventral margins in the present species during adult stages. We have measured 15 large specimens from each locality for our analyses. We have done all of the measurements, except the curved height, with digital slide calipers with a precision of 0.01 mm. Statistical analyses were performed with SPSS ver. 15.0 statistical software packages (SPSS ver. 15.0, licensed and registered to Palaeontology Division, Geological Survey of India, Kolkata).

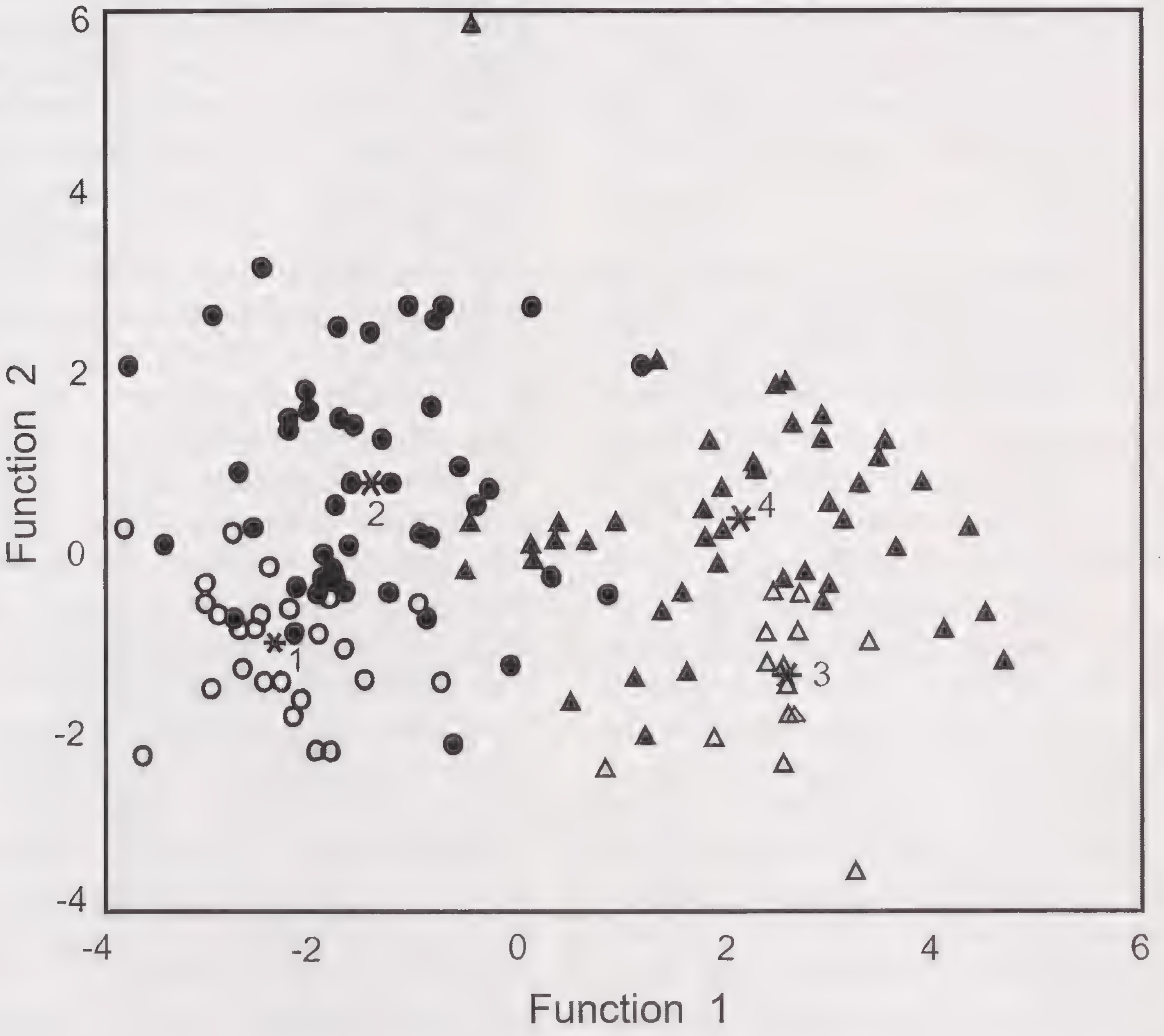

FIG. 3. Plot of all specimens on the first two functions of a four-group canonical discriminant function analysis. Circles represent *Barnea candida* and triangles represent *Pholas orientalis.* Open symbols represent allopatric populations and closed symbols represent sympatric populations.

TABLE 2. Loading of seven morphological characters onto the three discriminant functions of a four-group solution.

	Function 1	Function 2	Function 3
Shell length	0.636	1.742	-0.194
Shell height	-0.152	0.026	-0.782
Shell width	-0.228	0.465	-0.731
Posterior length	1.126	-1.989	0.409
Depth of pallial sinus	-0.052	0.369	-0.680
Curved height	-0.754	-0.699	1.480
Size of posterior muscle scar	-0.100	0.715	0.565
Total fraction of information explained	84.7%	14.1%	1.2%
Eigen value	4.31	0.82	0.08

RESULTS

The matrix generated by the Mahalanobis distances shows the relationships of the allopatric and sympatric populations of the species in terms of the relative distances between group centroids in reduced space. When we performed such an analysis on the four groups (sympatric and allopatric *Barnea candida* and *Pholas orientalis* populations), we found that these two species are more alike in sympatry than allopatry. The Mahalanobis distance and its F values of significance of the *Barnea candida* and *Pholas orientalis* populations are shown in Table 1. The F values indicate that, except in allopatric and sympatric populations of *P. orientalis*, the Mahalanobis distances are significant in 99% confidence level between all other populations. Mahalanobis D^2 based on all of the characters for allopatric populations of both of the species is 19.81. On the other hand, the Mahalanobis D^2 between the species in sympatry is 9.78. This significant reduction in Mahalanobis distance in sympatry than that of allopatry strongly suggests biological interaction leading to character convergence. Functions 1 and 2 of Figure 3 explain 84.7% and 14.1%, respectively, of all of the information. Table 2 shows loading of the original seven measures onto the three discriminant functions, along with their associated eigen values. It reveals that allopatric populations are separated mainly in shell length and curved height manifested by a wide separation along Function 1. The Mahalanobis distance between centroids of allopatric and sympatric *B. candida* is 3.67 (F value 8.75, significant at 99% confidence level), whereas that of *P. orientalis* is 1.25. This indicates that *B.candida* shifts more in sympatry than *P.orientalis*, and, as such, it is more dominant.

The contribution of individual measures onto the multivariate difference can also be expressed as univariate graphs. Table 3 shows the mean and standard deviations of all of the measures across all of the locations. Univariate plotting of individual characters also supports the result derived from multivariate analysis. Plotting of length data (Fig. 4) across all of the locations reveals that both species have shifted their character value in the presence of the other and have maintained nearly a fixed difference across all of the sympatric sites. It becomes apparent that in three sympatric areas (i.e., Dadanpatrabar, Shankarpur, and Chandipur), where they experience competition, their size comes reasonably close to Hutchinson's ratio (1:1.27 at Dadanpatrabar, 1:1.30 at Shankarpur, and 1:1.33 at Chandipur). This ratio indicates that these species maintain "an effective strategy for avoiding competitive elimination" (Clarkson, 1998: 49). Interestingly, the difference between the ratios is most pronounced between the allopatric zones (1:1.51), where they live separately. Figure 4, depicting the variation in depth of the pallial sinus, shows a parallel trend with that of length data. Their ratios in sympatry are again close to Hutchinson's values (1:1.25 at Dadanpatrabar, 1:1.31 at Shankarpur, 1:1.29 at Chandipur). Posterior length (Fig. 4) also shows a broad parallelism in sympatry. In Figure 4, which depicts variation in the size of the posterior muscle scar, the two species populations show strong convergence and the sympatric lines intersect.

The inflation graph (Fig. 4) shows strong convergence, and the shell convexity graph (Fig. 4) shows most of the sympatric values lying

TABLE 3. Means and standard deviations of populations of *Barnea candida* and *Pholas orientalis* at all sampled locations. L = Shell length; H = Shell height; W = Shell width; PL = Posterior Length; PS = Depth of pallial sinus; CH = Curved height and MS = Size of posterior muscle scar.

Population	L	H	W	PL	PS	CH	MS
Allopatric *Barnea candida*	61.7185 ± 5.26076	24.7922 ± 6.32157	22.9163 ± 2.39811	44.1415 ± 4.71454	32.9704 ± 5.17701	33.6667 ± 3.50823	27.9978 ± 7.20817
Allopatric *Pholas orientalis*	98.7486 ± 4.26422	28.5979 ± 1.40958	27.9100 ± 1.45028	78.0593 ± 2.70442	49.4693 ± 13.07397	40.7857 ± 2.19014	52.3293 ± 14.67749
Sympatric 1 *B.candia* Dadanpatrabar	79.1308 ± 6.39262	28.4775 ± 2.05778	27.1050 ± 2.86637	57.1700 ± 6.44202	42.3467 ± 3.95815	39.3333 ± 3.25669	58.4842 ± 6.39061
Sympatric 1 *P. orientalis* Dadanpatrabar	100.2327 ± 12.12219	30.4200 ± 2.79504	29.8947 ± 3.63078	76.3873 ± 10.23077	53.1173 ± 6.68241	41.0373 ± 4.74586	64.3527 ± 12.82142
Sympatric 2 *B.candida* Shankarpur	86.4700 ± 7.11863	30.4757 ± 2.87622	29.6186 ± 2.96508	56.9586 ± 5.49308	45.3086 ± 3.23614	42.9286 ± 5.29825	66.4950 ± 10.10476
Sympatric 2 *P. orientalis* Shankarpur	112.6293 ± 5.28341	33.4836 ± 1.93044	33.0386 ± 3.05858	84.3771 ± 6.10256	59.2114 ± 3.97846	46.2143 ± 3.42342	65.0593 ± 16.77995
Sympatric 3 *B.candida* Chandipur	65.2307 ± 4.25574	23.5233 ± 1.69910	23.2760 ± 1.70215	46.6333 ± 3.75431	35.9840 ± 2.79390	32.2667 ± 4.23365	37.0593 ± 12.48410
Sympatric 3 *P. orientalis* Chandipur	86.8960 ± 16.19034	26.6610 ± 4.17750	25.8500 ± 4.48648	65.8450 ± 13.90320	46.5680 ± 9.58034	35.1000 ± 6.52261	61.1040 ± 20.41541

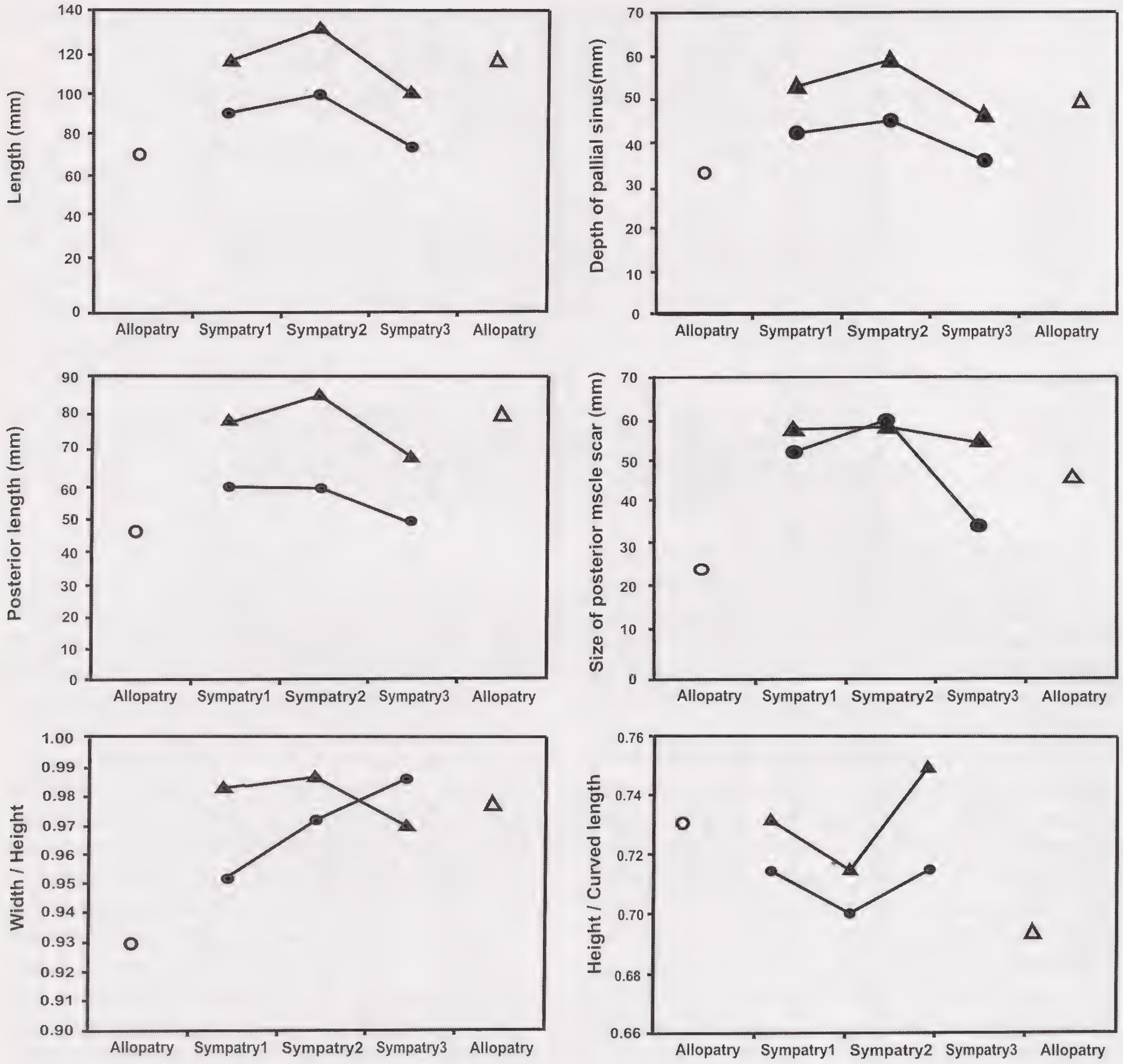

FIG. 4. Univariate plots of different shell morphologies in allopatric (open symbols) and sympatric (closed symbols) populations of *Barnea candida* (circles) and *Pholas orientalis* (triangles). Solid lines connect means of sympatric samples of each species.

intermediate between two extreme allopatric values, especially for *Barnea candida.* In different allopatric areas, this species shows high intraspecific genetic variability with respect to shell width and valve curvature. At Gangasagar, the average shell length of *B. candida* (mean 59.11 mm) is smaller than that at Bakkhali (mean 63.86 mm), but width/height and height/ curved height ratios are always greater. This suggests that these two characters are independent of size. However, in sympatry with competing *Pholas orientalis*, the values of these characters always show increasing trends indicating clearly the role of biotic interaction. *Pholas orientalis* shows a somewhat mixed reaction with respect to these two characters. In some sympatric areas, shell inflation remains more or less the same and in others, it slightly decreases or increases. However, it strongly reacts with respect to the shell curvature data. In all sympatric areas, *P. orientalis* diverges from its allopatric values and shows a high degree of shell streamlining. Overall, the shape data tend to show broad parallelism among the sympatric areas like those of the size-induced characters discussed above.

Mahalanobis distances between sympatric populations of *Barnea candida* and *Pholas*

TABLE 4. Distribution of specimens of *Barnea candida* and *Pholas orientalis* collected at all sampled localities.

	Bakkhali	Gangasagar	Dadanpatrabar	Shankarpur	Chandipur	Antervedi
Barnea candida	95	350	300	500	75	–
Pholas orientalis	–	–	75	155	15	350

orientalis were 12.43, 19.82, and 12.84, respectively, for Dadanpatrabar, Shankarpur, and Chandipur. Interestingly, Mahalanobis D^2 between each allopatric *B. candida* and *P. orientalis* population consistently had greater values. For example, D^2 between Bakkhali *B. candida* and Antervedi *P. orientalis* is 24.51 and Gangasagar *B. candida* and Antervedi *P. orientalis* is 29.23. At Shankarpur, shifting of *B. candida* from its allopatric populations (D^2 11.67 and 13.60, respectively, for Bakkhali and Gangasagar) is greater than that of *P. orientalis* (D^2 6.45 for Antervedi). On the other hand, at Chandipur, *B. candida* underwent less of a shift (D^2 1.68 and 1.38, respectively, for Bakkhali and Gangasagar) than did *P. orientalis* (D^2 4.01). At Dadanpatrabar, the Mahalanobis distances between allopatric and sympatric *B. candida* were 8.34 and 9.91, respectively, for Bakkhali and Gangasagar; the difference between allopatric *P. orientalis* and sympatric *P. orientalis* was 2.05. This pattern of asymmetrical convergence and varied degree of shifting of character values from allopatric populations shown by both species indicates that the degree of convergence is not only a function of the presence or absence of competition, but also is a function of the intensity of competition. The intensity of competition is manifested by the relative abundance of each species at each location (Table 4).

With the help of another observation of discriminant function analyses (Table 5), we can further confirm the finding that sympatric populations of both species come closer than in allopatry. We found that identification phase of this analysis correctly assigned the allopatric populations to their respective taxonomic groups. The re-identification was done in the discriminant analysis. In the DFA, the degree of success of classification is measured by calculating the error or misidentification rate (Shindel & Gould, 1977). The previously made groups, using qualitative characters of taxonomic identification and presence-absence data (i.e., the two species and allopatric and sympatric populations) were tested and re-allocated using the discriminant function calculated from the seven variables. It is seen that the error rate while discriminating between allopatric populations of *Barnea candida* and *Pholas orientalis* is always 0, whereas in the sympatric populations there is an overlap and the error rate increases to 6.7% and 11.1% respectively. This degree of overlapping can be attributed to morphological convergence in sympatry.

Because allopatric and sympatric populations of each species show morphological variation, we wanted to determine the variation of population structure of each species between allopatry and sympatry. We collected samples ranging from very small to very large size, and we

TABLE 5. Result of discriminant function analyses identification phase: hits and misses from rows (actual group membership) into columns (assigned membership).

	Allopatric		Sympatric	
	Barnea candida	*Pholas orientalis*	*Barnea candida*	*Pholas orientalis*
Allopatric				
Barnea candida	100	0	0	0
Pholas orientalis	0	86.7	0	13.3
Sympatric				
Barnea candida	22.2	0	71.1	6.7
Pholas orientalis	0	20.0	11.1	68.9

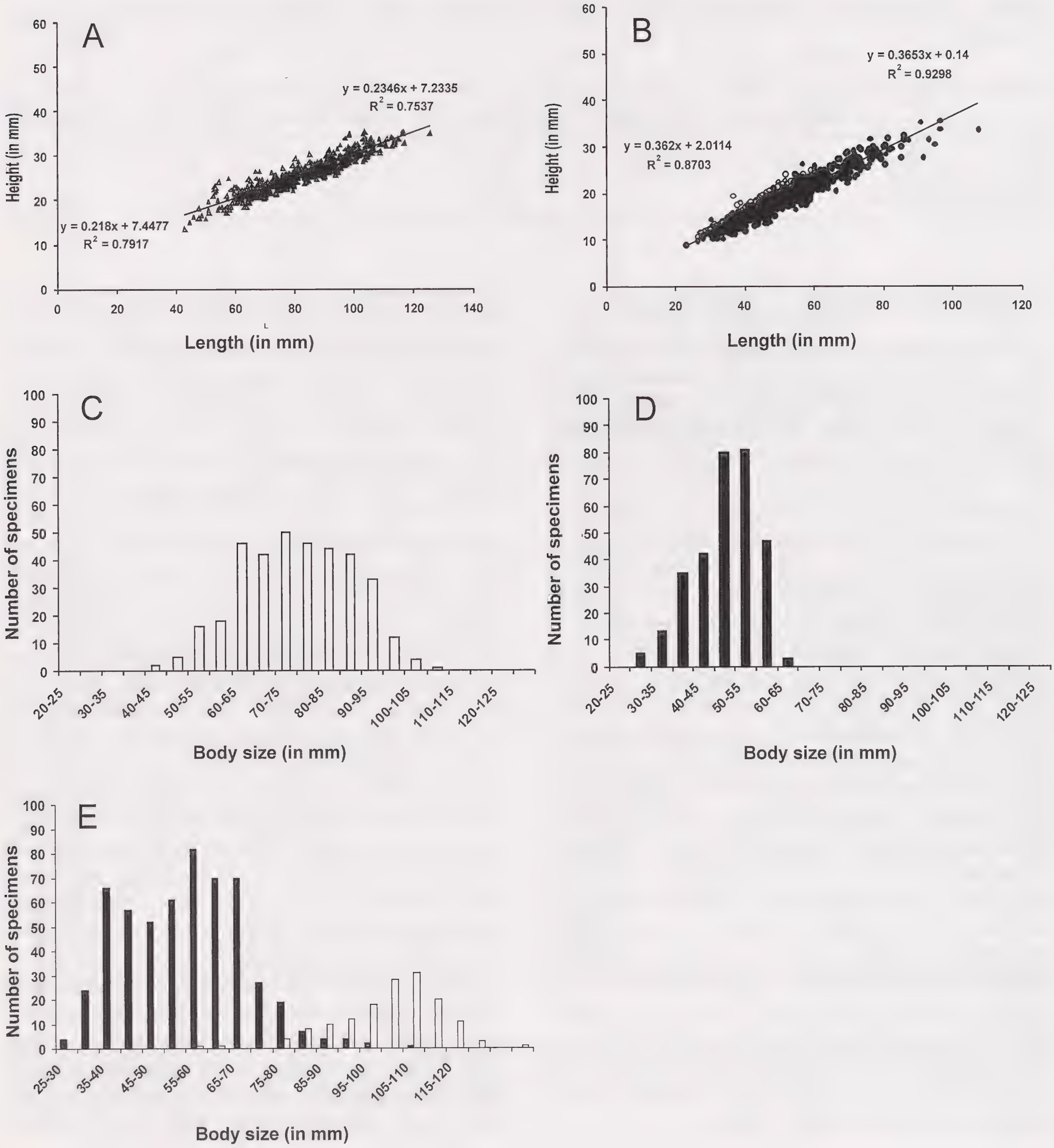

FIG. 5. Growth curves for allopatric (open symbols) and sympatric (closed symbols) populations for *Barnea candida* (A) and *Pholas orientalis* (B). Histograms of body size of specimens of both species in the same allopatric populations (Gangasagar for *B. candida* and Antervedi for *P. orientalis*) are shown in C, D, and E, respectively. Solid bars represent *B. candida* assemblages, whereas open bars represent *P. orientalis*. Locality details in Fig. 1.

performed bivariate analyses involving height and length (Fig. 5A, B), as well as histograms (Fig. 5C–E), to show distribution of each normal assemblage in different areas.

All of these analyses revealed that *Barnea candida* and *Pholas orientalis* have become morphologically closer to each other in sympatry, and they have diverged in allopatry. This convergence in sympatry is evident in both size and shape data.

DISCUSSION

In the south, where *Pholas orientalis* lives alone, the eastern Indian coast is a more exposed shore, whereas allopatric populations of *Barnea candida* are from sheltered areas belonging to the Sunderban delta. Therefore, it can be argued that the changes in body size and other shell characters could be due to nonbiological factors. There are examples where coastal populations show clinal variation due to differing degrees of water turbulence (Newkirk & Doyle, 1975; Peel, 1987) or temperature (Yom-Tov, 2001) and food. Clinal variation is seen mostly in epifaunal organisms. Mud-boring infauna, such as the present species, are protected within their domicile from water turbulence and can remain indifferent. Many other infaunal bivalves, living in either sympatric or allopatric areas of *B. candida* and *P. orientalis*, do not show size or other variation (Rao et al., 1991, 1992; Mahapatra, 2001). This suggests that there is little or no difference in the abundance or quality of food among areas (direct measurement of availability of food particles was beyond the scope of this study). Other than competition, the benthic community faces predation pressure, and therefore the degree of predation might also exert selection pressure resulting in morphological variation. The eastern coast of India has a high diversity of predatory marine animals, such as fishes, crabs, and gastropods (Rao et al., 1991, 1992). Bivalves are mostly preyed upon by carnivorous muricid and naticid gastropods. Many dead bivalve shells littering Indian coastal areas bear characteristic boreholes made by such naticid gastropods as *Natica* and *Polinices*, or commissural breakage (personal observation). These kinds of predatory marks have also been observed in other areas (Carriker & Yochelson, 1968; Vermeij, 1987). Among the more than 1,200 specimens we studied, not a single specimen shows evidence of boring (members of two genera of naticids have prey-specific diets and target mostly shallow burrowing bivalves living in sandy habitats). Although gaping bivalves are often attacked through the gape (Vermeij, 1980; Ansell & Morton, 1987), this is not the case here. *Barnea candida* and *P. orientalis* always live in a firm muddy habitat and remain in situ within deep protective borings and are not subject to substantial predation pressure from gastropods. It, therefore, appears that size and other morphological variation shown by the present two species in sympatry from their respective allopatric areas are mainly due to their own biological interaction.

Such size indices as shell length, depth of the pallial sinus, and posterior length, show maximum variation in sympatry. In the case of *Barnea candida,* shell length increases significantly from allopatric sites (Bakkhali and Gangasagar) to sympatric sites (Dadanpatrabar and Shankarpur, $p < 0.001$). Interestingly, shell length dose not vary significantly within these sympatric sites ($p > 0.001$). In the case of *Pholas orientalis*, shell length increases significantly at one sympatric area, that is, Shankarpur ($p < 0.001$); however, this reduction is not statistically significant ($p > 0.001$) at Chandipur. Univariate analysis shows broad parallelism in the distribution of shell length values among the sympatric populations of the two species (Fig. 4). However, at all sites, their shell length ratio remained close to Hutchinson's value. Pholadines are strongly inequilateral (posterior part much greater than anterior part); therefore, further elongation of the shell at sympatric sites, for example, at Shankarpur, also was manifested in an increase in posterior length (for *B. candida*, $p < 0.001$; difference is marginally insignificant for *P. orientalis,* $p > 0.001$). In asymmetrical boring bivalves, the posterior part is generally larger because it accommodates long siphons. The distribution of the depth of the pallial sinus also shows this broad parallelism with shell length in sympatry (Fig. 4). In the case of *B. candida*, the allopatric sites are not significantly different ($p > 0.001$) from one another. However, statistically significant difference ($p < 0.001$) exists between allopatric and sympatric sites. On the other hand, *P. orientalis* shows less variation in sympatry ($p > 0.001$). This perhaps, as mentioned earlier, is due to the fact that *P. orientalis* is less dynamic. In boring bivalves, especially in pholadines, there occurs a unique character shift, that is, the anterior adductor muscle scar migrates on the umbonal region. To minimize resistance against abrasion within the stiff substratum, they thicken their umbonal regions by refolding the shell, and in this process, they have lost their external ligament. Shifting the anterior adductor muscle on the umbonal region now helps the pholadine to open the valves, and it is functionally analogous to the didactor muscle in brachiopods (Pojeta, 1987). The posterior adductor muscle is now used alone to close the valves. Repeated opening and closing of valves occurs when the bivalves burrow within the substratum (Stanley, 1970). Therefore, a more powerful muscle is required to burrow more deeply. Sympatrically, both species have increased their muscle scar sizes, and we have already shown that they have also increased their shell length and depth of pallial sinus to access deeper substrata. At Shankarpur, where competition is most intense, they have almost identical muscle scar sizes.

From all of the statistical analyses, it is clear that *Barnea candida* and *Pholas orientalis* show morphological convergence in sympatry and divergence in allopatry. In most of the other cases, competition leads to divergent character displacement. This is because species reduce competition by partitioning such resources as food or space. Resource partitioning results in modification of characters of ecological significance. However, in the present study, this is not the case. Bivalves as a class have a specific diet. Being deposit or suspension feeders, bivalves could not reduce competition by food resource partitioning. The only other resource that the competiting species could reduce overlapping is the habitat. However, habitat segregation of the present two species is not possible for two reasons. First, they are mud borers and therefore cannot migrate to nearby sandy habitat. Secondly, the mud flats are spatially limited, found mainly near the estuary mouths. Because of these similar ecological requirements, the two species accommodate competition rather than avoid it. Because they are borers, they try to segregate the habitat vertically. However, in allopatric Bakkhali and sympatric Chandipur, *Barnea candida* lives at depths of 15 to 20 cm below the surface (Rao et al., 1991, 1992). There is no published data on depths of *P. orientalis* on the eastern coast of India, but elsewhere they are reported to bore to depths of at least 40% more than their shell lengths (Pinn et al., 2005). It appears that the two species have more or less the same depth limit within the substratum and therefore, when subjected to competition, they try to segregate by depth. This is evidenced by significant different depths of the pallial sinus.

It is already shown that the degree of convergence varies from place to place in the overlapping areas. At Dadanpatrabar and Chandipur, these two species show maximum convergence (D^2 11.30 and 12.91, respectively). Although degree of convergence is similar for these two areas, the reaction of each of the species is not very similar. At Chandipur, *Pholas orientalis* decreases shell length (Fig. 4) from the value of its allopatric populations, whereas *Barnea candida* almost remains neutral. At Dadanpatrabar, *B. candida* reacts more strongly by increasing shell length, depth of the pallial sinus, and posterior length, whereas *P. orientalis* stays more or less neutral. Relative population size of each species differs in sympatric areas. Although *B. candida* is always numerically superior in every site, the relative abundance of *P. orientalis* varies (Table 4). Because *P. orientalis* is very sparse at Chandipur, it appears that *B. candida* does not experience competitive pressure and therefore remains unchanged. *Pholas orientalis*, on the other hand, has significantly reduced its shell size over that of its allopatric population. At Chandipur, both species face steep competition for habitat from other deep-boring bivalves, such as *Sanguinolaria acuminata* Deshayes (1857), *Glauconome sculpta* G. B. Sowerby III (1894), and *Laternula truncata* Lamarck (1818) (Rao et al., 1991,1992; personal observation). Many of these species live deeper within the substratum; *L. truncata* burrows more than 1 m (Rao et al., 1991, 1992). Therefore, space left for the competing *P. orientalis* coincides with that of *B. candida.* At Dadanpatrabar, the other boring species are absent and *P. orientalis* is more abundant than at Chandipur. In many marine taxa, when habitat is a limiting resource, organisms tend to monopolize it (Raup & Stanley, 1978). They are, therefore, locked in severe competition in occupying this habitat. The only direction that they can move for ecological segregation is down into the substratum. From Fig. 4, it is clear that both species have become larger, more elongated with larger siphons, and show almost parallel trends in sympatry. The intensity of competition is best evident at Shankarpur, where each species has a robust population size; they are largest here, with deepest pallial sinuses. However, *P. orientalis* always remains relatively larger than *B. candida* and this way maintains better accessibility within sediments.

Barnea candida and *Pholas orientalis* have wide biogeographic distributions (Turner, 1969) and interestingly, an internet search (www.specimenshells.net, www.conchology.be, www.glaucus.org.uk, www.shell.kwansei.ac.jp) reveals that outside India they have allopatric distributions. We cannot assume that these website data are unbiased representations of body size distributions and are statistically robust. However, there is an anthropogenic bias that collectors often favour larger specimens (Roy et al., 2003), and these data may provide a baseline against which present body size distributions can be compared. Below we

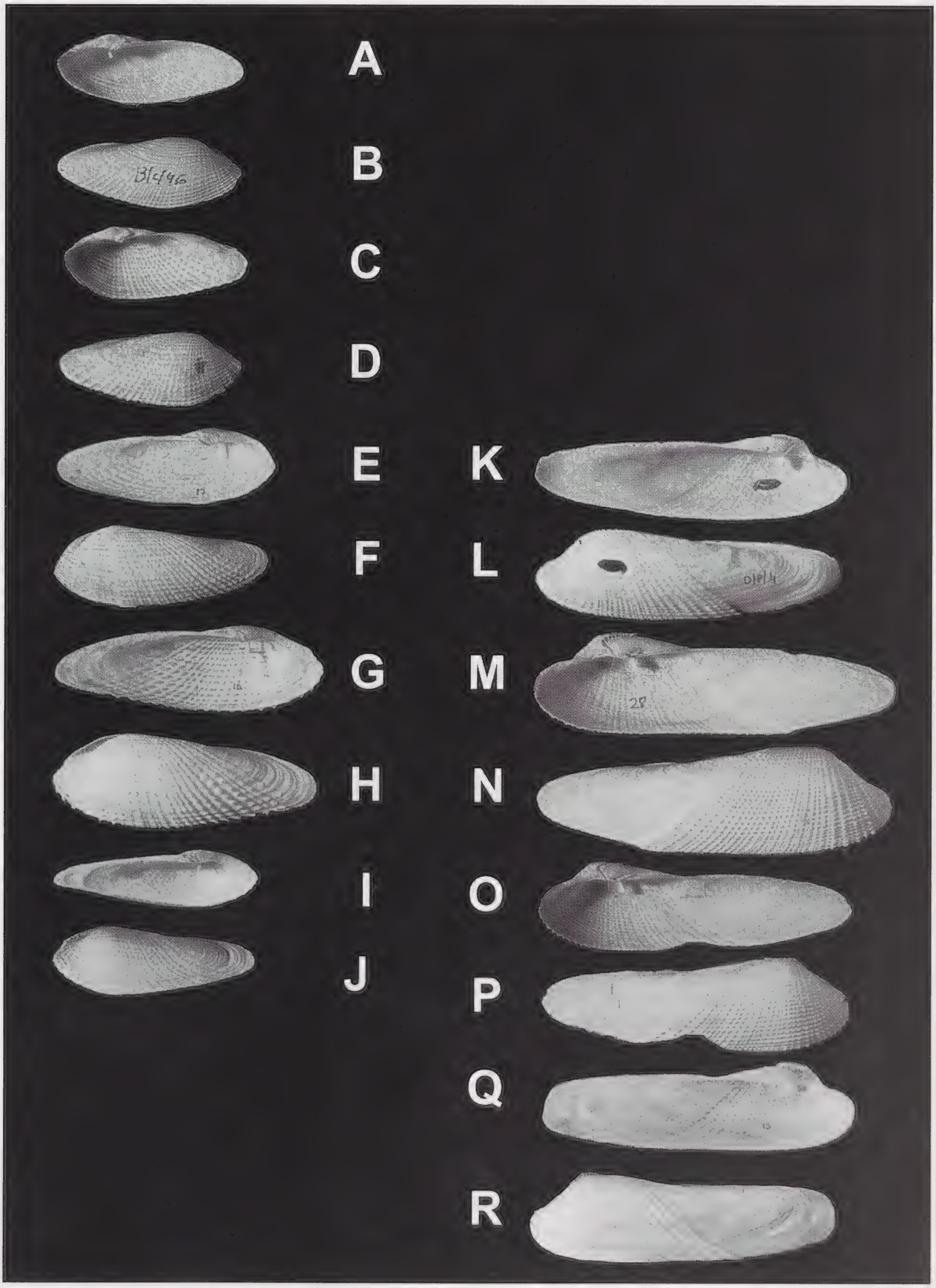

FIG. 6. Sympatric and allopatric populations of *Barnea candida* (left) and *Pholas orientalis* (right). Note that the shells of the two species are more similar in sympatry (compare E–J and K–P) than in allopatry (A–D and Q–R). The localities (also see Fig. 1) are: Bakkhali (A–B), Gangasagar (C–D), Dadanpatrabar (E–F and K-L), Shankarpur (G–H and M–N), Chandipur (I–J and O–P), and Antervedi (Q–R).

mention size ranges (if samples are few) and averages (if they are more than 10) provided by the websites. *Barnea candida* is mostly found in different areas in Europe, and their average size distribution is as follows. In France, body length ranges between 3.6 and 5.9 cm (www.conchology.be), whereas it ranges between 2.5 and 3.9 cm in England (www.glaucus.org.uk); maximum length in Spain is about 3 cm (www.shell.kwansei.ac.jp). Shell sizes of most of the European allopatric populations are smaller than the Indian allopatric populations, and in sympatric Shankarpur, India, the average length (8.6 cm) perhaps, is the greatest length recorded for *Barnea candida* in the world. Similar size ranges of *Pholas orientalis* in other areas also support this observation. Allopatric populations in Thailand (www.conchology.be) have average lengths of 9.22 cm, and in Singapore maximum length is 8.75 cm (Turner, 1969). These data are close to the size data of Indian allopatric distribution (9.87 cm at Antervedi). But, in the Philippines, the maximum size ranges from 11.2 to 13.4, cm with an average value of 12.2 cm (www.specimenshells.net; www.shell.kwansei.ac.jp). This is, however, slightly larger than the Indian sympatric value of 11.26 cm at Shankarpur.

All of the analyses reveal that both species show morphological variation between sympatric and allopatric populations. Bivariate growth curves (Fig. 5A), involving shell length and shell height, were performed to evaluate patterns of variation from early ontogeny. They demonstrate that the sympatric *Barnea candida* population has a smaller shell height value than that of the allopatric population, suggesting that competition has led this species to become more streamlined to penetrate deeper within substratum from early ontogeny. The bivariate graph of shell length and shell height also supports sympatric convergence, because growth trajectories come closer in sympatry than in allopatry.

Thus far, we have seen that the two species show morphological convergence in sympatry due to competition resulting from very similar ecological requirements (Fig. 6). However, other than food and habitable space, species try to avoid intraspecific hybridization (Schindel & Gould, 1977). At Gangasagar and Antervedi, the allopatric sites of *Barnea candida* and *Pholas orientalis*, respectively, and at Shankarpur, the main sympatric site, we have made fresh collections during June–August 2006. The histograms (Fig. 5C–E) of these populations reveal that the breeding seasons of the two species must be different. We have found smaller sizes of *B. candida* in allopatry and sympatry, suggesting that these monsoon months are the breeding season of *B. candida*. But we have not found any smaller samples of *P. orientalis* in sympatry, which are present in allopatry. It could be that there is a delay in the onset of the breeding season of *P. orientalis* in sympatry.

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